STUDIES IN THE GENUS GYMNOSPORANGIUM—I. NOTES ON THE DISTRIBUTION OF THE MYCELIUM, AND BUFFER CELLS, AND THE GERMINATION OF THE AECIDIOSPORE

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The sporophytic mycelium of different species of *Gymnosporangium* exerts an influence in connection with the growth of the tissues of the cedar hosts which is manifested in a variety of ways. It is not clear just why one species will cause the formation of a rather fleshy gall, while another species will lead to the development of a witch's-broom or a hard, woody burl. A study of the interrelationships of host and parasite, especially the more intimate association of the hyphae and the host cells may help to solve some of these interesting questions.

I wish to report briefly at this time the results of some studies made to determine: (1) the distribution of the mycelium in an infected leaf; (2) the possibility of its spread from leaf to stem; (3) the degree to which it spreads up and down; (4) its distribution in wood, phloem and cortex; (5) the distribution of haustoria. Four-nucleated aecidiospore germ-tubes of *Gymnosporangium transformans*, and the formation of buffer cells in the teleutospore sori of *G. fraternum* and *G. transformans* will be noted.

Farlow[1] determined the general distribution of the mycelium in the host for a number of American *Gymnosporangia* and described with considerable clearness the primary effects of the parasites on the tissues of the host plants. He found that the burls on *Chamaecyparis* infected by *G. biseptatum* are probably the result of a stimulation of the cambium by the hyphae mainly distributed in the cambium region. There appeared to be very little in the nature of a deleterious effect of the parasite on this host. It was evident to him, however, that the actual presence of mycelium in a given tissue is not necessary to account for distortions or abnormalities. In *G. Ellisii* the fungus interferes with the normal growth of the host, producing proliferations and swellings of the stems and branches. This may be due to a disturbance in the nutritive processes, the primary cause of which may

[1] Farlow, W. G. The *Gymnosporangia* or Cedar Apples of the United States. Am. Mem. Boston Soc. Nat. Hist. 1–38. *pl. 1, 2.* 1880.

lie at some distance. Farlow noted that the hyphae of this species are exceptionally large and that the brown mycelium runs down into the wood and along the medullary rays and also makes other brown patches extending some distance in circular areas between the annual rings. The greater part of the mycelium is found near the cambium and large masses of it are collected at points in the bark in preparation for the formation of sori.

Wörnle[2] made an extensive study of the relationships of host and parasite in nine species, and his report published in a forestry journal furnishes a valuable contribution on the subject. He endeavored to determine the particular tissues with which the mycelia are associated and stated his conclusions with considerable positiveness. *G. Juniperinum* was of special interest to him inasmuch as he supposed that the sori found on leaves as well as those on small twigs belong to the species that produces larger sori on the main stems. He could see that the mycelium in an infected leaf was connected with that from a small twig. He also learned that the leaf form is perennial. Four successive cork callus formations were found in one case, showing that for four years a sorus had been developed at the same point on the leaf. In the stem-inhabiting type he found that the mycelium is present in the wood as well as in the bast and cortex. Radially placed strands of parenchyma accompanied by mycelium are common in the wood; "Schlafende Augen" he calls them. Hyphae are intercellular, and he noted in some cases the presence of haustoria. Although Wörnle was not himself clear regarding the relationship of the three forms of the rust which he called *G. Juniperinum*, he was inclined to believe that the fungus gains entrance through the leaves, the mycelium later running down the twigs and into the main stem, where it becomes firmly established. Fischer[3] has shown that this was a false assumption since Wörnle was dealing with at least two species, but the accuracy of Wörnle's observations is not questioned.

The mycelium of *G. clavariaeforme*, according to Wörnle, is not present in the wood, although considerable transformation of tracheid tissue is to be seen in infected stems; arcs and sectors of this tissue are replaced by parenchymatous cells. He found, however, no mycelium in such areas. As the mycelium is generally distributed in the cortex and bast, he assumes that the cambium is in some way stimulated to develop more than a normal amount of wood cells, some

[2] Wörnle, P. Anatomische Untersuchung der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forst. Nat. Zeits. 3: 68–84, 129–172. 1894.

[3] Fischer, E. Studien zur Biologie von Gymnosporangium juniperinum. Zeits. Bot. 1: 683–714. *f. 1–8.* 1909; 2: 753–764. 1910.

of which are inhibited in their growth, lacking bordered pits and having thin walls, that is, are more in the nature of parenchyma. Wörnle was especially fortunate in having the opportunity for consultation with Hartig and Tubeuf in his work, but he was handicapped in studying American species by being restricted to a limited number of dried specimens. He agrees in the main with Farlow's account of the location of the mycelium in *G. biseptatum* and *G. Ellisii*, although he makes no mention of Farlow's work. He concludes further that the mycelium of *G. biseptatum* is intercellular and is entirely absent in the wood. The tracheids are somewhat irregular and have thinner walls than ordinarily. He found that the hyphae of *G. Ellisii* are about 8 μ in diameter and are present in the wood, bast and cortex. The brown hyphae are associated with brownish cells which together make easily recognizable patches. The mycelium here also is strictly intercellular. His study of a three year old stem of red cedar infected with *G. clavipes* disclosed the fact that the tissues of the host are only slightly affected. The mycelium is distributed not only beneath the sorus but in the whole periphery of the twig, especially in the bast region. The wood is entirely free from the fungus. Wörnle predicted that this rust must develop sori one year after inoculation because in this three-year-old stem he found traces of two former sori, one above the other.

Harshberger's account[4] of the relationships of hyphae and host cells deserves special consideration, inasmuch as it does not agree in certain important particulars with the statements made by Farlow and Wörnle. He finds that in *G. biseptatum* the mycelium is quite generally present in the wood region where he states the hyphae are for the most part strictly intracellular. They run down through the lumen of a tracheid, pass out through bordered pits, enter an adjacent tracheid, or move over to medullary ray cells which they penetrate and thus become established where they receive nourishment sufficient to maintain their perennial growth as the wood of the burl increases in diameter. He believes that the hypha actually in the lumen of the cambium cell is responsible for the stimulation of this cell to produce abnormal amounts of wood! He describes and figures these intracellular hyphae in much detail, especially the hyphae in longitudinal sections of wood. The explanations accompanying his figures leave no doubt of Harshberger's opinion regarding the identification and location of intracellular hyphae. He lays much stress on the presence of "plugged" tracheids. He believes that they are caused by the mycelium with which they are generally asso-

[4] Harshberger, J. W. Two Fungous Diseases of the White Cedar. Proc. Acad. Nat. Sci. Philadelphia **1902**: 461–504. *pl. 22, 23.*

ciated. Hyphae may sometimes be intercellular. Swollen and nodular hyphae are not infrequent. Harshberger questions whether haustoria are ever present. It is well known from the work of Hartig and others that hyphae of wood-destroying fungi are capable of boring through lignified cell walls. Such fungi obtain their nourishment by activities leading to the disorganization of wood cells. The rusts are highly parasitic and haustoria play an important part in their nutrition. It would be interesting to find that such trunk parasites as *G. biseptatum* and *G. Ellisii* are more like the common heart rot fungi than they are like other rusts where the hyphae crowd in between the cells or mass in the intercellular spaces. My own observations do not support several statements made by Harshberger.

Gymnosporangium Ellisii

I have succeeded in infecting *Chamaecyparis* by spraying potted cedars with aecidiospores of *G. Ellisii* (*G. myricatum*). Several cedars naturally infected and bearing brooms of different ages have also been grown in pots, so that I have had an abundance of material in all stages of growth for study.

The sorus usually matures about twenty-one months after inoculation. Where young leafy branches have been infected we find that the sorus may break out either in the leaf axil or through the leaf itself. At this time there is very little distortion of the twig. The primordium of the axial sorus is partly in the tissue at the base of the leaf and partly in the stem cortex beneath. Where the sorus emerges through the leaf we find that there is an increase in the number of mesophyll cells and the sorus primordium is not far below the epidermis. Strands of hyphae can be traced down to the short vein and into the woody portion of the stem. Serial sections show that the mycelium does not travel up and down the stem very rapidly; in some cases only one or two cm. in the first two years. Where a rapidly growing main stem is infected the hyphae run as much as five cm. in the same time. Trunks thirty years old have been cut and one such shows traces of mycelium for a vertical distance of only about ten cm., although the fungus had been active during the life of the tree, thirty years. Sections taken from various parts of a small artificially infected plant bearing a dozen potential witches' brooms show that each broom will be the result of a separate infection. The mycelium does not enter at one point and spread through the entire plant. However, if the original infection should be at the growing point of the main stem a broom is formed that permanently dwarfs the plant. The mycelium invades every tissue except the cork. It is fo nd in patches in all of the annual rings, and is espe-

cially abundant along some of the medullary rays. It is not evenly distributed. The hyphae seem to travel in fascicles and they are everywhere intercellular. Sections of the wood show that there are strands of parenchyma that, from appearances, would seem to be burrowing through the wood, thrusting the tracheids aside as though endowed with great power. These same parenchyma strands are also found in the cortex. They run in almost every direction. Hyphae are always associated with them. Tracheids in infected areas of the wood are considerably modified. The walls are thinner, the cells are prismatic and in many cases have failed to develop bordered pits. The walls of such cells frequently appear to be broken down or crushed in and partially disorganized. It may very well be that the fungus has some power to disorganize lignified cell walls. Wherever hyphae occupy the lumen of a cell it is likely to have been the result of such mass action. There is no boring through the walls nor entering tracheids through bordered pits. The "Schlafende Augen," or parenchyma strands, in the cortex and along the line of medullary rays in the wood as well as the patches of abnormal or partially developed tracheid tissue are the result of the stimuli proceeding from hyphae that were nearby at the time this tissue was being developed. It is difficult to understand how a cambium cell harboring a hypha could divide at all, or how a tracheid could change its form once it has become lignified.

The cambium reacts in such a way as to cut off by the excessive development of tracheids certain fascicles of hyphae and thus check the radial and longitudinal advances of the fungus. The apparently isolated patches of mycelium found in the heart wood are nevertheless quite generally connected above or below with some radially placed strand that ultimately reaches the cortex. This may be the main reason why one finds living hyphae deeply imbedded beneath several rings of wood.

Haustoria may occasionally be found in cells of the cortex medullary rays, but they are not abundant. Some of these haustoria are binucleated.

There seems to be no question that Wörnle was right in stating that the hyphae of *G. Ellisii* are intercellular.

Gymnosporangium biseptatum

Harshberger and Wörnle disagree on a second important point in their studies of *G. biseptatum*. This relates to the presence or absence of mycelium in the wood cylinder of the cedar.

I have as yet been unable to infect the cedar with this species. I have studied specimens naturally infected and especially one from a

small plant which I was able to transplant and grow in the greenhouse. In 1915 this small burl bore two sori. The same burl bore six sori in 1916. The branch was six years old when cut. The mycelium spreads quite evenly through the cortex and is especially abundant beneath a sorus where we find one or two large haustoria in nearly every cortex cell. The medullary ray cells of the cortex are likewise attacked and the mycelium penetrates down to the cambium. The walls of the tracheids are somewhat thicker than usual, in this respect differing from the specimens examined by Wörnle.

I have been unable to find any intracellular hyphae, and in this six-year-old branch there are certainly no hyphae inside of the cambium ring, that is, in the wood cylinder, such as Harshberger describes. The most striking feature about this fungus is the great abundance of large haustoria found in nearly every cell of the cortex in the vicinity of a sorus.

Gymnosporangium clavipes

The red cedar may be infected with *G. clavipes* without difficulty by spraying with aecidiospores. Plowright[5] states that it takes two years for *G. clavariaeforme* to mature sori, but Tubeuf[6] found that sori developed one year after inoculation of the juniper. My experience with *G. clavipes* may serve to explain this discrepancy.

On August 1, 1915, a small cedar was inoculated with *Gymnosporangium clavipes*. A few sori appeared in 1916 on what was, in 1915, the growing region of the main stem. In 1917 sori burst out quite generally over the plant. The question has arisen: Is it possible that from the original point of infection of 1915 the mycelium ran down the main stem out into the branches where further sori formed in 1917? Inspection showed that the sori were not evenly scattered along the branches, but appeared in groups with intervening spaces of some length between, varying from one to several cm. Serial sections of some of the smaller branches made at points between groups of sori do not show the presence of mycelium. For several inches near the top of the main stem the sori are so close together that mycelium appears to be continuous. It is noteworthy, however, that there are no sori on those parts of the plant that have grown since the plant was inoculated in August, 1915. The mycelium is intercellular and lies for the most part well out in the cortex just beneath the cork, some hyphal ends even pushing in between the inner cork cells. It may require only one year for full development at the

[5] Plowright, C. B. British Uredineae and Ustilagineae. 1893.

[6] Tubeuf, C. Mitteilungen über einige Pflanzenkrankheiten. Zeitschr. Pflanzenkr. 3: 201–205. 1893.

growing point where abundant food is available, or even take two years in regions less favorably located. The characteristically binucleated haustoria are of large size and are easily demonstrated.

I have examined several stems three years old but do not find that the mycelium spreads out through the entire cortex and into the bast as described by Wörnle. *G. clavipes* brings about less increase in development of wood tissue than *G. biseptatum*, but this may be due to the fact that the mycelium does not approach the cambium as closely. This species may develop strictly foliicolous sori in which case the mycelium is very limited in extent. The sorus is then not deep seated. Haustoria can be found in epidermal cells.

Gymnosporangium transformans

I have previously reported[7] that two leaf-inhabiting species of *Gymnosporangium* can be distinguished on *Chamaecyparis*. The account of the cultures in support of this statement is being published in another paper. For convenience I shall call one form *G. transformans*. Its aecidial form is *Roestelia transformans* on *Aronia*. *Gymnosporangium fraternum* is an appropriate name for the second leaf form which infects *Amelanchier*. The aecidium is very similar to that of *Roestelia Botryapites;* I am not prepared to prove that it is *R. Botryapites*. A cytological examination of cedar leaves infected with *G. transformans* and *G. fraternum* reveals further characteristics by which they may be distinguished.

If we section a leaf of *Chamaecyparis* infected with *G. transformans*, we find that the mycelium is especially abundant in the large intercellular spaces of the spongy mesophyll and the hyphae push in between the cells of the palisade on all sides. No hyphae are to be found in the epidermis. If the section includes the short vein of the leaf we see that hyphae are prevented in some way from entering the vascular tissue. There is an irregular row of large cells surrounding the vein of the leaf. These pericycle(?) cells do not normally form a perfectly closed ring; it is occasionally broken by smaller supporting cells. In regions where the hyphae reach the large cells one can find, here and there, that they have been penetrated by one or two haustoria. Such infected cells are about one third larger than usual. The cytoplasm is rather dense, including considerable stored food and takes the gentian violet stain somewhat deeply. The nuclei appear to be quite normal. Haustoria are also occasionally found in mesophyll and palisade cells. The cells of the mycelium are binucleated and the nuclei stand out very clearly, especially where

[7] Dodge, B. O. Report on further cultures of Gymnosporangia. Paper read at the December meeting of the Botanical Society of America, New York, 1916.

leaves have been fixed at a time when the sorus is fully matured. The mycelium is confined to the leaf bearing the sorus and does not ordinarily invade the stem at any point along the line of attachment. The large cells surrounding the leaf vein appear to prevent the mycelium from entering the phloem of the stem.

At the point where the sorus is to be developed, we find a well-defined pseudo-parenchyma, the cell walls taking the orange stain. The upper cells of this pseudo-parenchyma are somewhat enlarged and elongated. These are likewise binucleated. They soon begin to swell, lose their cytoplasm, and the nuclei degenerate. In order to show these upper cells in this condition the material must be fixed at the earliest possible time that an infected leaf can be distinguished,

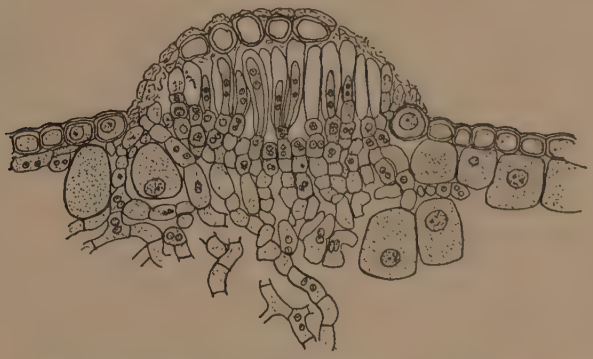
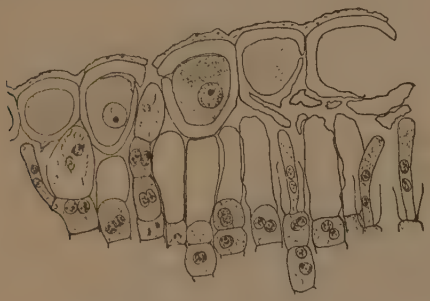


FIG. 1. Section of a sorus of *G. transformans* on a leaf of the southern white cedar at the narrowest portion of the young sorus. The epidermis is broken up on either side, only traces of the cuticle and fragments of the cell walls being visible. At the center epidermal cells are still visible. A number of buffer cells in various stages of degeneration can be seen, and binucleated teleutospore buds growing through the buffer cells are common.

that is, when a spot appears as a slight, waxy, translucent, light orange blister. In such cases the epidermis may not have been ruptured and fixation of the mycelium is not apt to be of the best, unless the leaf is cut through. The upper cells mentioned become mere bladdery sacs and during this process of swelling the inner walls of the epidermal cells, and hypodermal cells when present, are broken down either by enzyme action or by actual pressure, and the heavily cutinized epidermis is lifted up and split open (Text-fig. 1). The splitting usually occurs in a line along one side of the leaf, but very often the split runs longitudinally down through the middle. Sometimes two sori develop side by side on the same leaf. The bladdery cells evidently function as buffer cells to disrupt the epidermis. These buffer cells perhaps represent simply the first series of teleutospore mother cells

that are sacrificed in order that the epidermis may be broken open (Text-fig. 2). The true basal cells now grow out through the buffer cells, forming a club-shaped bud which soon becomes binucleated. These nuclei divide and the stalk is cut off; later three pairs of nuclei can be seen and the wall is formed between the two cells of the teleutospore (Text-fig. 3). Quite mature spores can be found along the line where the epidermis first ruptures and all stages in their development can be seen further back.



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3

FIG. 2. A portion of a sorus of *G. transformans* showing two rather pointed buffer cells forcing epidermal cells aside, fragments of the walls of the epidermal cells lie just above the buffer cells at the right. Four young teleutospore buds are visible.

FIG. 3. Teleutospore of *G. transformans*.

The gametophytic stage on *Aronia* may sometimes attack the young stem, giving rise to an irregular herbaceous gall, which becomes covered with horn-like projections from which the aecidia arise. If such a plant is kept in the greenhouse all winter, aecidiospores will continue to be formed in some cases for several months after the leaves have fallen from the plant. These spores are regularly binucleated and possess 7 or 8 germ pores irregularly distributed (Pl. I, Fig. 1). The spores germinated on agar or water frequently form a swollen pouch near the tip of the germ tube. The nuclei of the spore push through the germ pore, apparently one closely following the other (Pl. I, Fig. 3). At the next stage we find two nuclei lying in the germ tube just outside of the pore (Pl. I, Fig. 4). These nuclei then migrate further out into the tube and come to lie in the swollen pouch (Pl. I, Fig. 5) where they presumably divide conjugately, since many cases have been observed where there were four nuclei, in pairs, lodged in this portion of the tube (Fig. 6). The germ tube now elongates rapidly and branches freely at the tip (Fig. 8). The four nuclei move forward and may lie along the tube in a row in the wider portion at the end or they may be distributed, one nucleus in each branch, or

two lying further back, the other two occupying separate branches. A cell wall is finally laid down, cutting off the outer portion of the germ tube containing the nuclei and most of the cytoplasm (Figs. 8–10). This curious method of germination is in no sense similar to the development of a promycelium, though four nuclei are produced in each case. It may be that it is fairly common among the rusts as Sappin-Trouffy has pointed out.[8] Whether or not it is possible to find an appropriate artificial medium for the development of the mycelium of a rust in artificial cultures, it would seem that such cases as these afford at least a starting point. Four-nucleated germ tubes are the rule in these cultures, but fully developed tubes with only two nuclei are not difficult to find (Fig. 11).

In some of my cultures in which the petiole of a leaf had been infected at the junction with the blade, it was found that the winter bud was larger than usual. The mycelium must have run down the petiole and become established in the bud. When such plants were put in the cold frame over winter and taken out in the spring, these buds developed small leaves which at once became evenly covered with spermogonia and later were transformed into large galls from which aecidia developed quite normally.

In some cases the mycelium seems to penetrate into the tissues of the stem where a spindle-shaped swelling or burl is formed. In the following spring a green gall bursts out through the cork, forming a nodular swelling outside and from this spermogonia and aecidia are produced. I have had several cases in which *Roestelia transformans* has survived the winter and developed aecidia the following spring The same is true in my cultures of *R. Botryapites*. In October, 1915, winter buds of six Amelanchiers showed signs of being infected. All of these survived the winter and developed spermogonia and ripened aecidiospores in the month of June, which is several months earlier than they can be found in nature. These are not cases where the formation of an aecidium has simply been delayed. On the contrary, an entirely new crop of spermogonia arises from newly formed tissue, new gall growth, and we find the aecidia developing as in normal cases of infection with sporidia.

Gymnosporangium fraternum

The buffer cells in the teleutospore sori of *G. fraternum* are much more striking in appearance, forming as they do a perfectly even palisade layer that frequently extends entirely across the sorus without interruption (Text-fig. 4). This is a very characteristic feature of

[8] Sappin-Trouffy, P. Recherches histologiques sur la famille les Urédinées. Le Botaniste 5: 59–244. *f. 1–69.* 1 D 1896.

the rust. The difference in the shape of the buffer cells of *G. transformans* and *G. fraternum* corresponds roughly with that between the teleutospores; they are comparatively long in the latter species.

On January 30, 1917 a potted plant naturally infected with *G. fraternum* was taken from the cold frame and examined. Several leaves showed by the presence of slight yellowish spots that they would develop sori. Sections of one leaf cut on this date showed

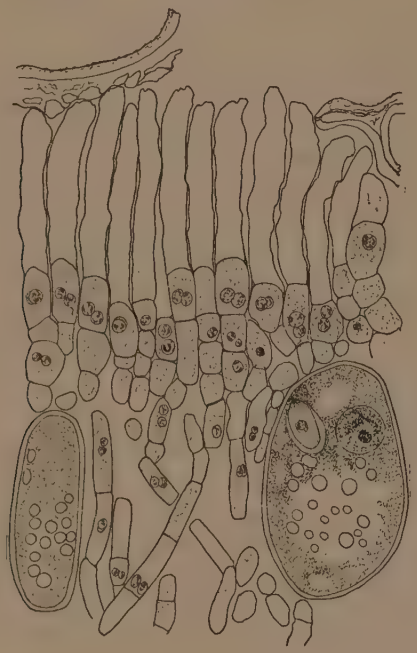

FIG. 4. Section of a leaf of the white cedar infected with *G. fraternum* showing the layer of buffer cells at the time when the epidermis has been quite completely disorganized. At the right a large palisade cell in the process of disorganization, but the nucleus is still visible and a haustorium is present.

that the pseudo-parenchyma or teleutospore primordium was well marked. The buffer cells were mostly without granular contents and nuclei (Text-fig. 5, *A*). In a few cases fragments of the degenerated nuclei could be seen. By February 2, a sorus taken from the leaf of the same plant showed great numbers of teleutospore buds in the 2- and 4-nucleated stages (Text-fig. 5, *C*). A few buds had 6 nuclei, and the stalk cells of these had been cut off. Buffer-cell walls were just visible as narrow irregular lines showing most distinctly at the base of the young teleutospore. Two days later, February 4, cross-walls had been formed in many spores but nuclear fusion had

not occurred (Text-fig. 5, *D*). Remnants of buffer-cell walls were now difficult to find. A mature spore is shown in Text-figure 5, *E*.

The mycelium of *G. fraternum* penetrates through the leaf in every direction. The mesophyll cells are usually somewhat enlarged and are packed rather closely together with small intercellular spaces. Haustoria are quite abundant in such cells. The cells surrounding the vein are especially affected. They appear to be filled with minute granules and as many as eight or ten haustoria can be found in a single cell, the more common number being two to four. A complete ring of these large cells is formed. This is due to an increase in number as well as their larger size. This, taken in connection with the increase in the mesophyll tissue, gives the leaf a slightly thicker and more compact appearance. The mycelium does not invade the

FIG. 5. *a*, pseudoparenchyma with buffer cells; *b*, 2-nucleated stage of the young teleutospore; *c*, 4-nucleated stage; *d*, 6-nucleated stage with cross walls; *e*, small spore after nuclear fusion.

vascular tissue even to the extent of penetrating the phloem of the stem. Both *G. transformans* and *G. fraternum* are capable of producing sori two or three years in succession, the latter may produce a sorus even after the leaf has apparently died. While haustoria are more numerous and attack the individual cells more vigorously in the case of the latter species, *G. transformans* seems in some way to be more destructive, as infected leaves more frequently die after maturity of the first sorus. Of the two species, *G. fraternum* is clearly the more nearly related to *G. biseptatum*, both from the nature of their teleutospores and the similarity of the aecidia in the two species. If the mycelium of *G. fraternum* is ever able to push in beyond the large cells surrounding a vein and get into the central cylinder of the stem, therefore nearer the cambium, we should look for a stimulus such as

might lead to the formation of a greater amount of wood tissue such as we find in the burl of *G. biseptatum*. *G. fraternum* has almost constantly 2-celled teleutospores, 3-celled spores are exceedingly rare. In *G. biseptatum* 3- and 4-celled spores predominate. I should be highly gratified to learn that the change in environment from the leaf to the stem, or more exactly from cortex to phloem, by the fungus could bring about such a decided change in the structure of its spores.

EXPLANATION OF PLATE I

Gymnosporangium transformans

Stages in the Germination of the Aecidiospores. × 750

FIG. 1. A binucleated spore.

FIG. 2. The germ tube has pushed out, the nuclei are still within the spore and do not show appreciable change in form.

FIG. 3. One nucleus is crowding through the germ pore, the other lies beneath. The "pouch" is formed just back of the tip of the germ tube.

FIG. 4. Both nuclei have escaped from the spore and lie just outside of the germ pore.

FIG. 5. Two nuclei lie in the expanded portion of the germ tube.

FIG. 6. Four nuclei are plainly visible in the "pouch." The germ tube has not begun the second stage of its growth.

FIG. 7. Tip end of fully developed germ tube showing four nuclei in a row.

FIGS. 8 and 9. Other fully developed germ tubes showing a more pronounced type of branching.

FIG. 10. The germ tube has made about the maximum growth of which it is capable under artificial conditions, a cross wall cuts off the main portion of the granular cytoplasm at the forward end of the germ tube.

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